GAMETOPHYTE OF PELLIA EPIPHYLLA

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(WITH PLATES I–IV AND ONE FIGURE)

Three of the species of *Pellia*—*P. epiphylla*, *P. calycina*, and *P. endivaefolia*—show morphological differences, especially with respect to the apical cell, which would suggest a generalized or possibly an unstable ancestral form. No detailed study of any of these species has been reported. During the investigation upon which this account is based, it has been found that in *P. epiphylla* not only are there transitions in the method of growth, but also that the development of the antheridium may follow any one of several divergent lines.

Antheridium

It has been generally accepted that "the antheridium of *Pellia* is larger than that of *Aneura*, but its development is very similar, except that the stalk is multicellular, as it is in other *Anacrogyneae*."[1] In addition to this method of development, *P. epiphylla* shows young antheridia having characters of Marchantiales; moreover, the spermatogenous initials may be cut out in the same way as the primary axial cell of the archegonium.

The division of a dorsal cell, the third or fourth from the apical cell, by a horizontal cross-wall is the first evidence of an antheridial initial. The outer of the two cells formed divides again, giving the three cells of the antheridial row—the basal cell, the stalk initial, and the outer cell; the latter by successive divisions gives rise to the wall cells and spermatogenous cells. Meanwhile, the dorsal cells, immediately surrounding the antheridial group, divide and become papillate, thereby producing a ring-shaped involucre (figs. 2, 3). The outer cell of the antheridial group divides next. The position of the wall is significant; if it is vertical and median,

[1] CAMPBELL, D. H., Mosses and ferns. New York. 1905 (p. 92).

the successive divisions follow an antheridial sequence; if, however, the wall is inclined and somewhat removed from the central position, the cell divisions which follow are similar to those of a developing archegonium. In the former case the vertical wall is followed by a curved wall on either side, which cuts the vertical wall as shown in figs. 7 and 8. Two similar walls, rotated about the central axis through an angle of 90° (figs. 8, 9), complete the separation of the peripheral region from the central spermatogenous region. The first two of these walls may be nearly parallel at the base (fig. 7), or they may be at right angles; similarly the second pair. Such an antheridium is characteristic of the Jungermanniales.

Occasionally the outer cell, mentioned above, is divided into quadrants by walls at right angles to the vertical wall (figs. 10, 11), in which case four wall cells are cut off by periclinal divisions, giving also four spermatogenous cells. The process is similar to that characteristic of *Sphaerocarpus* or Marchantiales.

Fig. 14 illustrates the result of a combination of these two methods of development. In fig. 15 is shown a double antheridium; the two halves have become completely separated by the vertical division and each has developed independently. The process may be compared to the characteristic development of the double antheridia of Anthocerotales.

When the first wall formed in the outer cell is inclined and somewhat removed from the median position, it is followed by a second and a third wall, each of which is similarly placed, but revolved with respect to each other through an angle of 120° about the vertical axis (figs. 17, 18, 26, 27, 28). A transverse wall divides the central cell into the cap cell and the spermatogenous initial (fig. 19). The characteristic archegonial development is followed until the massive spermatogenous group begins to be formed (figs. 22, 28), instead of the axial row.

Occasionally this critical third wall of the antheridium is inclined inward instead of outward, as described above (fig. 23). Two walls similarly inclined complete the separation of the peripheral region from the central spermatogenous initial (figs. 24, 25). This form is similar to that last described with the exception of the inclination of the walls and the resulting lack of the cap cell.

The differences in these antheridia are emphasized by the fact that in the first form (fig. 8) there are two spermatogenous initials, paired as in Jungermanniales; in the second form there are four, arranged in the form of a quadrant (fig. 10), as in Marchantiales; and in the third and fourth there is but one spermatogenous initial (figs. 10, 24, 25).

That the structures described above are developing antheridia, and not archegonia, is evidenced by their position and by the presence of an individual involucre. The antheridia are single and dorsal, while the archegonia are grouped in the terminal pocket.

Archegonium

The position of the archegonial group is of considerable morphological importance. CAMPBELL, with reference to the work of JANCZEWSKI, states: "The archegonia are formed in groups just back of the apex but he [JANCZEWSKI] does not seem to have been able to detect any relation between them and the apical cell such as obtains in *Aneura*, but it is possible that such a relation does exist." As mentioned above, the archegonia are terminal and inclosed in a "pocket," which is formed by a cup-shaped involucral growth. As will be described more fully, the archegonia arise from an apical group of cells, any of which may become an archegonium initial. There is no regular succession in the formation of archegonia; apparently old and young organs are indiscriminately intermingled. Since the apical group ceases to function as such after the production of archegonia, *P. epiphylla* may be regarded as truly acrogynous. The involucre is produced by cells which are cut off laterally by the apical group (fig. 40), and pushed out very much as the wings during the previous period of growth; in this event, however, the lateral cells are forced out on all sides to form a complete inclosure.

The structure and development of the archegonium conforms, in general, to the characteristic liverwort form. Some specific characters may be noted.[2] "After the archegonial mother cell is cut off it does not divide at once by vertical walls, but a pedicel is first cut off [fig. 31]; after which the upper cell undergoes the

[2] CAMPBELL, D. H., Mosses and ferns. New York. 1905 (p. 90).

usual divisions." This character serves to emphasize the similarity which exists between the archegonium as shown (figs. 31–33), and the antheridium (figs. 16–21). Except for the position and presence or absence of the involucre, these organs would be difficult to differentiate until the spermatogenous group or the archegonial axial row, as the case may be, begins to develop. The cap cell gives rise to a group consisting of more than the usual number of cells. The first division of the cap is often simultaneous with the division which gives rise to the primary neck canal cell and the primary ventral cell (figs. 32, 35), and four cap cells may appear in cross-section when there are but three neck canal cells and a ventral cell (fig. 36). Fig. 38 shows a group of cap cells, 6 in cross-section, which may be compared with those which form the neck of the archegonium of Filicineae. JANCZEWSKI reports that the number of neck canal cells may be as high as 16 or even 18; 9 is the greatest number seen by the writer (fig. 38). The venter becomes massive before fertilization; it may be 2 or 3 cells in thickness; a many-celled stalk is also formed (fig. 37). In the young archegonium the neck has usually only 5 vertical rows of cells. The cells originating from the third wall cell do not divide until the archegonium approaches maturity (fig. 39).

Methods of growth

A certain form of apical cell may usually be given as characteristic of a genus or even of a larger group. In *Pellia*, however, there is no such conformity; the apical cell of *P. calycina* has four cutting faces, two lateral, a dorsal, and a ventral—the cuneate apical cell. The dolabrate apical cell of *P. endivaefolia* has but two cylindro-convex cutting faces; while that reported as characteristic of *P. epiphylla*, the lenticular cylindric apical cell, has a posterior convex and two lateral cutting faces. In the last named species, however, there are several methods of growth; these cannot be sharply delimited, but for clearness five rather distinct forms may be taken as characteristic of successive periods of growth.

During the time of intra-capsular gametophytic division a massive body is formed. There is no regional growth, but all cells have an equal power of division. This period of growth is of short duration. The gametophyte body retains this massive form until after the resting period.

The second period of growth begins by the formation of a cuneate apical cell. A terminal cell is cleft by a wall inclined about 30° with reference to the longitudinal axis of the spore; a second inclined wall bisects the first at an angle of approximately 90°; lateral walls complete the cuneate apical cell (fig. 41). The latter cuts off dorsal and ventral segments (fig. 42) as well as lateral segments (fig. 43). Such a method of growth is characteristic of the young gametophyte until about the time of antheridium formation.

The growth of the third period is by means of a lenticular cylindric apical cell (fig. 47). The transition is somewhat irregular. Sometimes the apical cell is more or less equally divided; then the two halves simultaneously cut off cells (fig. 45) which correspond to the dorsal and ventral segments of the preceding form. The thallus in cross-section has the appearance of being medianally divided by a wall. Another transition form is shown in fig. 44. As the thallus becomes thicker the posterior angle becomes greater, the two faces being finally replaced by one which is curved. The cells cut off from the posterior face divide rapidly; as many as 6 segments may be formed before the next division occurs. The rapid division of the laterally placed cells causes the wings to be protruded outward and forward (figs. 46, 48, 49). There has been much discussion regarding the method of branching. HOFMEISTER[3] believed that the central papilla ("Mittellappen") shown in fig. 14 was the seat of the chief apex; hence that there is no true dichotomy. LEITGEB[4] states that the origin of the central papilla is from a marginal cell. When branching takes place, the apical cell, instead of cutting off a lateral segment, divides equally or almost so; each of these daughter cells assumes apical characters. The central papilla is produced by the crowding together of lateral segments from the two apical cells. It later develops into a central lobe corresponding to fused wings. Branching is essentially

[3] HOFMEISTER, W., Higher Cryptogamia. Ray Society. 1862.

[4] LEITGEB, H., Untersuchungen über die Lebermoose. 1882. Vols. II and III. Jungermannieen.

dichotomous; although the thallus may appear to have a central axis along the main line of growth, it is a matter of comparative rapidity in growth rather than origin. This form of apical cell is continued throughout the antheridial period.

The fourth period of growth is terminal and regional; it is concerned with the production of the archegonial pocket. The cells surrounding the original apical cell assume the power of cutting off lateral and posterior segments. The region of growth is in the form of a terminal disk. Lateral segments are crowded out on all sides to produce the continuous, cup-shaped involucre. A cross-section in any plane is similar to a horizontal section through the growing region at the time of branching (fig. 49). This growth is checked by the production of archegonia; any of the surface cells of the pocket may produce an archegonium (fig. 40). About the time of fertilization the last period of growth begins.

Any further growth is in connection with the developing sporophyte. Starch accumulates in the cells surrounding the foot and a massive growth takes place. Usually only one sporophyte develops in each pocket; a rather thick calyptra is formed about it, and sterile archegonia are carried along; these are to be seen attached to the surface of the calyptra. The first growth of the gametophyte is massive, similarly the last.

Relation of antheridium and archegonium

The relationship of the various forms of antheridia and their relation to the archegonium is demonstrated by the occurrence of antheridia in a single species, *Pellia epiphylla*, which are similar in development to each of these organs. The Marchantiales condition is generally to be found among the first antheridia; the Jungermanniales form is most dominant at the middle period, occurring, however, throughout the complete antheridial period. The archegonial form is usually found among the last antheridia to be produced. There is an evident time relation between these forms. Moreover, one may be regarded as derived from another through a series of progressive sterilizations (text fig. 1).[5] In the form

[5] Cf. HOFMEISTER, The higher Cryptogamia. Untersuchungen über die Lebermoose. Vol. II (*Pellia*).

characteristic of Marchantiales (figs. *A*, *B*, *C*), the vertical median wall (1) is followed by two walls (2 and 3) at right angles to the former, thereby forming quadrants (*A*, *B*, *C*, *D*). Four periclinal walls (4, 5, 6, 7) form a sterile wall cell and a spermatogenous cell

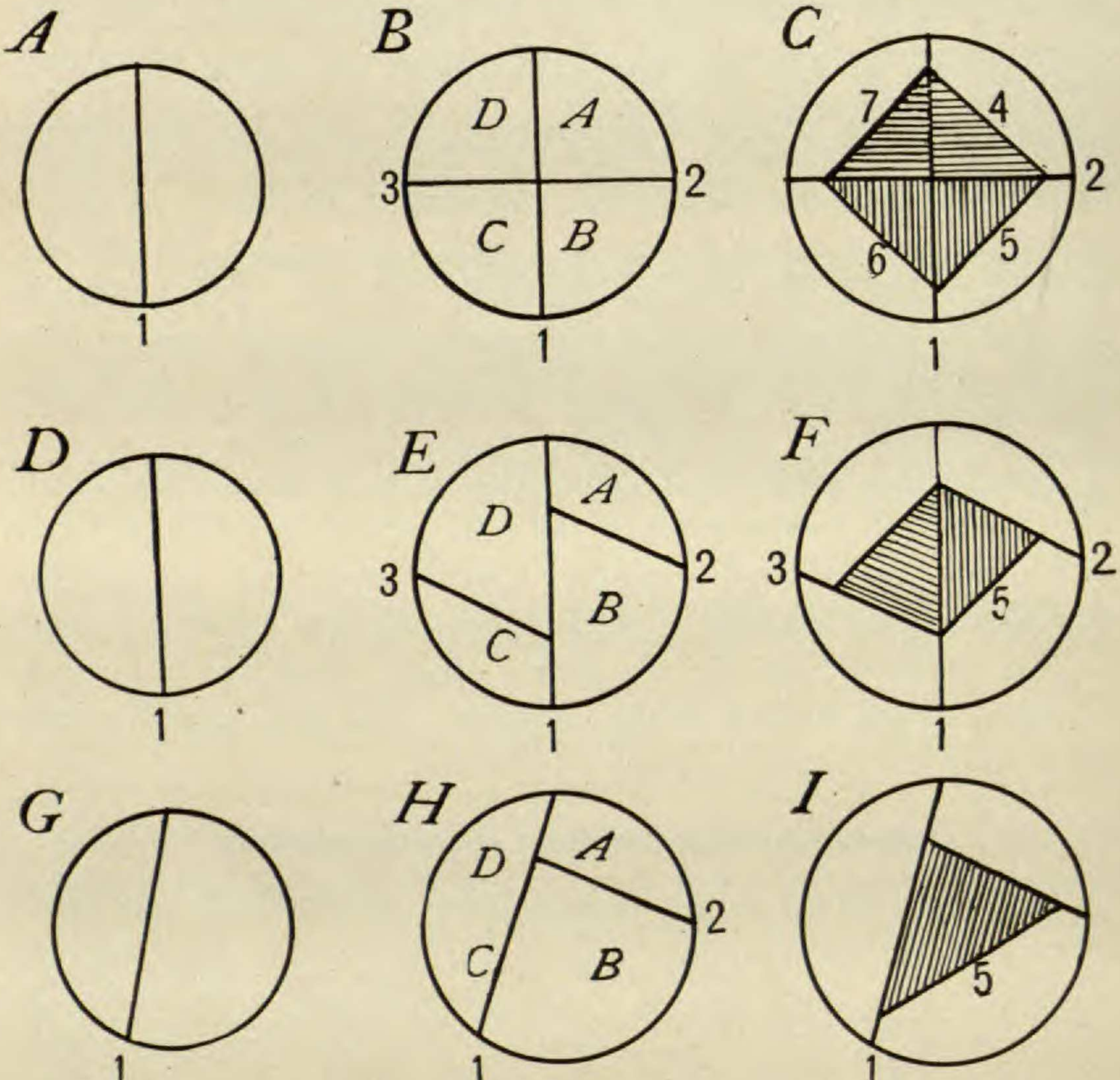


FIG. 1.—Explanation in text

from each quadrant. In the Jungermanniales form (figs. *D*, *E*, *F*) the median vertical wall is followed by two walls corresponding to the second and third above, but somewhat inclined (2, 3, fig. *E*). Periclinal walls (5, 7) form two centrally placed spermatogenous cells. The quadrants *A* and *C* have become sterile wall cells; only the quadrants *B* and *D* give rise to spermatogenous cells. In the archegonial form (G, H, I) the first wall (1) is not median, but somewhat laterally placed and inclined; there is no wall no. 3; the section corresponding to the quadrants C and D does not divide, but remains as a sterile wall cell. Wall 2 again cuts off a section corresponding to quadrant A, which also persists as a sterile wall cell. A periclinal wall (5) divides the section corresponding to quadrant B into a wall cell and a spermatogenous cell. Three of the quadrants have become sterile. Starting with the Marchantiales form of antheridia, by the sterilization of alternate quadrants the Jungermanniales form is derived; and by the sterilization of three quadrants the archegonial form results. The sterilization sequence corresponds to the time sequence as described above.

Only one step is lacking in this series to complete the transition from the antheridium of Marchantiales to the archegonium, namely the reduction of the spermatogenous mass into a single row of cells, only one of which, the egg, shall be functional. Such transition forms have been described by DAVIS[6] in Marchantiales. The writer has seen such "archegonia" with gamete masses in sections prepared by Dr. W. J. G. LAND. *The antheridial forms of P. epiphylla furnish evidence that the various types of antheridia and the archegonium have had a common origin*, possibly gametangia resembling in structure the antheridium of Marchantiales.

Relationships

The genetic relationships of *P. epiphylla*, because of its diversity, present a rather complex problem. With respect to its relation to other species of the genus *Pellia*, if the other species retain throughout life the form of apical cell ascribed to them, it would follow that *P. epiphylla* has branched sooner from the general line of progress and has retained and developed generalized characters. As a member of the Jungermanniales, this species is acrogynous in the sense that growth is checked, apical growth is stopped, by the production of archegonia. It differs from the more characteristic Acrogynae in having several regions of growth, each of which is checked in the same way. It is possible that acrogyny

[6] DAVIS, B. M., The origin of the archegonium. Ann. Botany 17: 477–492. 1903.

has been reached by several lines of development; hence close relationship with "Acrogynae" is not necessarily implied. If the development of the antheridium may be taken as a basis of classification, it would seem that *Pellia* arose from the main line of advance before the two branches, Jungermanniales and Marchantiales, became separate, even before the archegonium and antheridium became definitely differentiated in their methods of development.

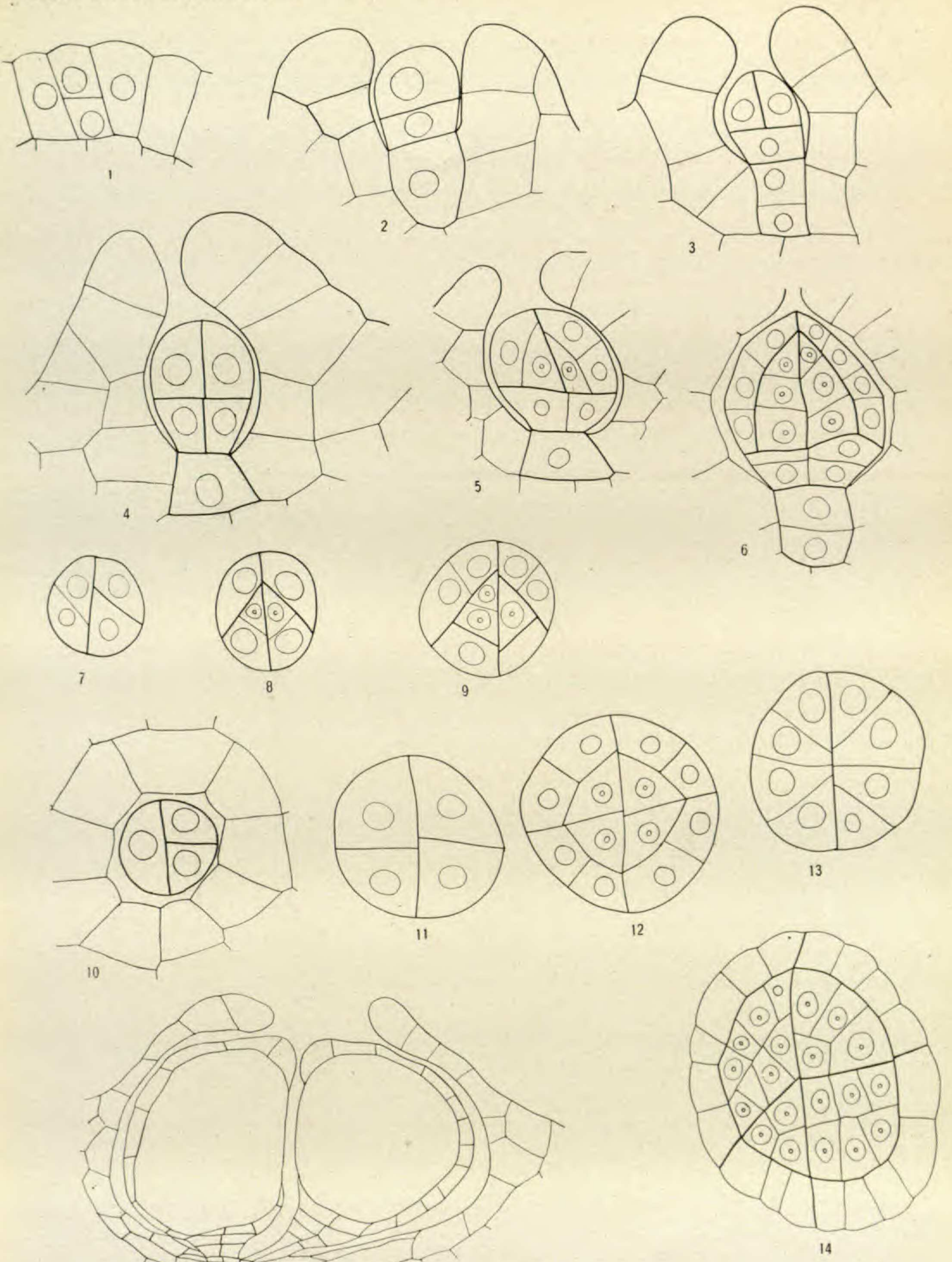
From *Pellia* we have evidence regarding the relation of Jungermanniales and Marchantiales. There is in the life history a transition from the cuneate apical cell of Marchantiales form to the lenticular cylindrical apical cell found in certain Jungermanniales; similarly, the antheridium, already discussed, affords strong evidence for the existence of such a relation. The evidence tends to indicate that Marchantiales are primitive and that Jungermanniales are derived.

Summary

The antheridium.—The development varies. The dominant method is that characteristic of Jungermanniales; forms occur, not infrequently, which are like the antheridium of Marchantiales, while others are like the archegonium in their early development.

The archegonium.—The archegonia are produced from cells of the apical group and occur in an archegonial pocket. The diversities from the regular form are few; the large number of neck canal cells, the extreme development of the cap, the frequent reduction of the number of tiers of neck wall cells to five, and the somewhat massive venter may be noted. The outer cell of the two resulting from the division of the archegonial initial divides horizontally before the vertical wall is formed.

Methods of growth.—Several periods of growth may be recognized, each having a specific method of growth: the massive; the period of the cuneate apical cell extending until antheridium formation; the period of the lenticular cylindric apical cell, or the antheridial period; the period of regional apical growth, or the period of archegonium production; and the second period of massive growth, or the period of sporophyte dependence.



HUTCHINSON on PELLIA